A COMPARISON OF *PORPHYRA DIOICA* SP. NOV. AND *P. PURPUREA* (ROTH) C. AG. (RHODOPHYTA: BANGIOPHYCIDAE) IN EUROPE

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ABSTRACT — This paper describes two species previously confused under the name *Porphyra purpurea* (Roth) C. Ag. sensu lato: *Porphyra dioica* sp. nov. and *P. purpurea* sensu stricto. The holotype (BM) of *P. dioica* is from Sidmouth, Devon, England and the proposed neotype (BM) of *P. purpurea* is from Nord-Ost Watt, Helgoland. *Porphyra dioica* is characterised by having olive-green to purple-brown, frequently laciniate, lanceolate to broadly ovate fronds which fold in half when held vertically; it is dioecious with marginal sori; spermatangial packets contain 64 spermatangia; carposporangial packets contain 8 carpospores. *Porphyra purpurea* sensu stricto is characterised by having brown to reddish-brown, usually entire, elliptical to obovate fronds; it is monoecious with male and female sori separated by a distinct line; spermatangial packets contain 64-128 spermatangia; carposporangial packets contain 16 carpospores. Carpospores of both species develop into a filamentous "*Conchocelis*"-phase. Ecological differences are also apparent, with *P. dioica* occurring in the lower midlittoral of more exposed shore regions, and *P. purpurea* in the midlittoral of more sheltered locations.

RÉSUMÉ — Cet article décrit deux espèces qui ont été confondues jusqu'à maintenant sous le nom *Porphyra purpurea* (Roth) C. Ag. sensu lato : *Porphyra dioica* sp. nov. et *P. purpurea* sensu stricto. L'holotype (BM) de *P. dioica* provient de Sidmouth, Devon et le néotype proposé (BM) pour *P. purpurea* vient de Helgoland. *Porphyra dioica* se caractérise par des frondes de couleur olive à pourpre-brun, fréquemment laciniées, lancéolées à largement ovales, qui se plient en deux quand on les tient verticalement ; l'espèce est dioïque, avec des sores marginaux ; les spermatocytes contiennent 64 spermaties ; chaque zygote donne 8 carpospores. *Porphyra purpurea* sensu stricto se caractérise par des frondes brunes à brun-rougeâtre, généralement entières elliptiques à subovales ; l'espèce est monoïque, les sores males et femelles étant séparés par une ligne distincte ; les spermatocystes contiennent de 64 à 128 spermaties ; chaque zygote donne 16 carpospores. Les carpospores de ces deux espèces ce développent en un stade "*Conchocelis*" filamenteux. Des différences écologiques ont été mises en évidence - *P. dioica* se trouve dans le bas du médiolittoral des régions littorales plus exposées, tandis que *P. purpurea* se trouve dans le médiolittoral de localités plus abritées.

KEY WORDS: algae, Rhodophyta, Bangiophycidae, *Porphyra dioica*, *Porphyra purpurea*, morphology, *Conchocelis*, typification, nomenclature.

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INTRODUCTION

The highly variable morphology of members of the red algal genus *Porphyra* has led to considerable difficulty in defining some species. In this paper we define two species of *Porphyra*, that had previously been confused under the name of the type of the genus *Porphyra purpurea* (Roth) C. Ag. sensu lato: *Porphyra dioica* sp. nov. and *P. purpurea* sensu stricto.

A failure to distinguish between these two species has led to considerable taxonomic confusion since the species *Porphyra purpurea* was erected. *Porphyra umbilicalis* (L.) J. Ag. is also involved in the confusion, but our studies of its type and other relevant material are not yet complete. One of the consequences of this is that the exact distribution of these species remains uncertain. *Porphyra purpurea* sensu lato has been recorded for the northern Atlantic from Iceland and northern Norway to southern Spain and Portugal (South & Tittley, 1986) and throughout eastern Canada (Bird & McLachlan, 1992) to USA (Maine) (Stiller & Waaland 1996). Records from the northern Pacific, however, are now recognised as referring to a new species, *P. kurogii* Lindstrom (Lindstrom & Cole, 1992b).

The problem is further compounded by nomenclatural problems, details of which are beyond the scope of this paper. The name *Porphyra umbilicalis* (L.) Kütz. f. *laciniata* (Lightf.) J. Ag. used in the first preliminary Check-list of British marine algae (Parke, 1953) was taken from Kylin (1944). In her classic studies in the Bangioideae, Drew (1954) stated that the plants she used were similar to that from the Swedish west coast figured by Kylin (1944, Taf. 1, fig. 2) under this name.

Drew used the name 'without acknowledging the identity of this material with *Porphyra laciniata* of C. Ag. (1824) or *Ulva laciniata* of Lightfoot (1777)'. Her herbarium was presented to the Natural History Museum and the approximately 100 specimens of *Porphyra* have provided not only an insight into her species concepts, but also further data for ours. Subsequently, Kornmann (1961) equated Drew's material with *Porphyra purpurea* (Roth) C. Ag., which he found commonly on Helgoland and so this name replaced *P. umbilicalis* f. *laciniata* in later check-lists (Parke & Dixon, 1964; 1968; 1976; South & Tittley, 1986).

Strong evidence that there was more than one species under the name *P. purpurea* (Roth) C. Ag. was presented by Kornmann & Sahling (1991). They gave descriptions of these species as *P. purpureo-violacea* (Roth) Krishnamurthy (1972), following Krishnamurthy (1972) who had found that the epithet *purpurea* was illegitimate, and *P. laciniata* (Lightfoot) C. Ag. Their descriptions, however, were not based on type specimens. The basionym of *P. laciniata* is *Ulva laciniata* Lightfoot (1777), the type of which has long been known to belong to the Delesseriaceae (Dixon, 1959) and was finally identified as *Erythroglossum laciniatum* (Lightfoot) Maggs & Hommersand (1993).

Recent work by McGregor (1992) and McGregor & Lewis (1994) supported Kornmann & Sahling's (1991) view. Lindstrom & Cole (1993) provided further evidence to suggest that there was more than one species under the name when they reported that they had obtained two different zymograms and noted that *P. purpurea* is represented in the literature by different chromosome numbers. We agree with these authors that resolution of the problem requires reference to type material. Brodie *et al.* (1996) produced molecular and morphological evidence that two species were involved but indicated that there were problems with both the names they used.

In this paper, we have selected types for *P. purpurea* and *P. dioica*. In a separate paper (Irvine & Brodie, 1997), a proposal to conserve the binomial *P. purpurea* for *P. purpureo-violacea* has been made, since the former name has been used in the *Code* (Lanjouw *et al.*, 1956; Greuter *et al.*, 1994) for the type species of the genus *Porphyra* nom. cons. for 40 years. Combinations based on *Ulva laciniata* Lightfoot cannot be used for the other species under discussion since the type is not a *Porphyra*. No existing name has been found to apply to it, either, so it is described here as a new species, *Porphyra dioica*.

A considerable amount of data has been published for reputed *P. purpurea* (Lindstrom & Cole, 1992a, 1992b, 1993; Liu *et al.*, 1994; Mitman & van der Meer, 1994; Oliveira *et al.*, 1995; Ragan *et al.*, 1994; Reith & Munholland, 1993; Stiller & Waaland, 1996). However, a reassessment of material identified as *P. purpurea* is beyond the scope of the present paper.

MATERIALS AND METHODS

Material for morphological investigation was fixed in 4% formalin/seawater. Sections were made by hand. Staining of fixed material was as follows: 1% aqueous aniline blue was applied for between 1 and 5 min, mordanted with 5% HCl for approximately 10 s then mounted in 50% Karo® (commercial corn syrup) on microscope slides. Photographs were taken on a Nikon microscope with camera attachment.

Specimens examined for morphological work

P. dioica: Rhosneigr, Anglesey, 18.xii.1954, collected by (coll.) K.M. Drew (no. 2684, BM); Cruden Bay, Aberdeenshire, 26.i.1995, coll. L. Terry; Rottingdean, Sussex, 12.iv.1995, coll. J. Brodie; West Runton, Norfolk, 10.viii.1995, coll. J. Brodie; Lynton, Devon, 24.ix.1995, coll. S. Allison; Dunraven Bay, Glamorgan, 24.ii.1996, coll. J. Brodie; Rhosneigr, Anglesey, 14.iv.1996, coll. J. Brodie; Whitesands Bay, Cornwall, 5.v.1996, coll. J. Plumb; Sidmouth, Devon, 14.ix.1996, coll. J. Brodie; West Dale, Pembrokeshire, 2.xi.1996; Fanore, Co. Clare, Ireland, 17.vii.1995, coll. J. Brodie; Vágar, Sørvágsfjørdur, Faroes, 16.vix.1995, coll. K. Gunnarsson & R. Nielsen (no. F951288 03 20910); Düne, Helgoland 23.viii.1995, coll. J. Brodie; Madalena, Portugal, x.1995, coll. I. Sousa Pinto.
Porphyra purpurea: Seabrook, Nr Hythe, Kent, 9.viii.1956, coll. K. Drew (no. 2885, BM); Coombe Martin, Devon, 26.ii.94, coll. J. Brodie; Lilstock, Somerset, 28.ii.1994, 9.vi.1994, coll. J. Brodie, 18.vi.1996, 24.viii.1996, coll. J. Plumb & D. Gough; Borth, Cardiganshire, 10.iv.1994, coll. J. Plumb; Clevedon, Somerset, 2.v.1994, coll. J. Brodie; Gann Flats, Dale, Pembrokeshire, 29.viii.1994., coll. J. Brodie; Brixham, Devon, 1.ix.1995., coll. J. Brodie; Battery Point, Portishead, Somerset, 13.ix.1995, coll. J. Brodie; Dunraven Bay, Glamorgan, 24.ii.1996, coll. J. Brodie; Pegwell Bay, Ramsgate, Kent, 25.ii.1996, coll. I. Tittley; Sidmouth, Devon, 14.ix.1996, coll. J. Brodie; Fanore, Co. Clare, Ireland, 31.vi.1994., coll. J. Brodie; Eysturoy, Funningsfjord, Faroes, 11.ix.1995, coll. K. Gunnarsson & R. Nielsen (no. F951272 02 20773); Nord-Ost Watt, Helgoland, 24.viii.1995, coll. J. Brodie.
Abbreviations follow Holmgren *et al.* (1990).

The "*Conchocelis*"-phase for both species was initiated from spores released by the blade phase. Small pieces of blade (approximately 2.5 mm^2-5 mm^2) bearing carposporangia selected by eye were placed in pasteurised seawater at 15°C, 16:8 h, light:dark cycle.

Spores released were inoculated onto glass microscope slides and cultured in seawater enriched with 100% Von Stosch nutrient solution according to the methods of Brodie & Guiry (1988). Specimens from which "*Conchocelis*" was initiated: *P. dioica*, Cruden Bay, Aberdeenshire, 26.i.1995, coll. L. Terry (JB culture no. 167); *P. purpurea*, Lilstock, Somerset, 28.ii.1994, 9.vi.1994, coll. J. Brodie (JB culture nos 121 & 127).

RESULTS

Porphyra dioica sp. nov.

Diagnosis

Lamina non plerumque translucentia, lanceolata vel late-ovata, ad 270 mm longa et 270 mm lata, 48-80 µm crassa, in suspenso verticali in duabus partibus aequalibus longitudinaliter plicata, nonnumquam laciniata laciniis per findens formatis, olivacea vel purpureo-brunnea, monostromatica, cellulis a viso superficiali 10-16 µm in diametro, in sectione transversale 30-40 µm altae et 12-14 µm latae. Thalli dioecii soris semper marginalibus circum 2/3 laminae partes distales insertis; sori spermatangiali eburnea, massis 24-28 µm x 14-16 µm a viso superficiali, quoque 64 spermatiis instructis; sori carpogoniali extensi rubro-brunnei, massis 19-22 µm x 17-20 µm a viso superficiale quoque 8 carposporangiis instructis. "Conchocelis" *filamentosus.*

Blade not typically translucent, lanceolate to broadly ovate, up to 270 mm long and 270 mm broad, 48-80 µm thick, folding in half longitudinally when held vertically, sometimes laciniate, laciniae formed by splitting, olive-green to purple-brown; monostromatic, cells 10-16 µm in surface diameter, 36-40 µm tall by 12-14 µm broad in transverse section (TS). Thalli dioecious; sori always marginal around the upper two-thirds of the blade; spermatangial sori yellowish-white, spermatangial packets, 24-28 µm x 14-16 µm in surface view, containing 64 spermatia; carpogonial sori extensive, reddish-brown, carposporangial packets 19-22 µm x 17-20 µm broad in surface view, containing 8 carpospores. "*Conchocelis*" filamentous.

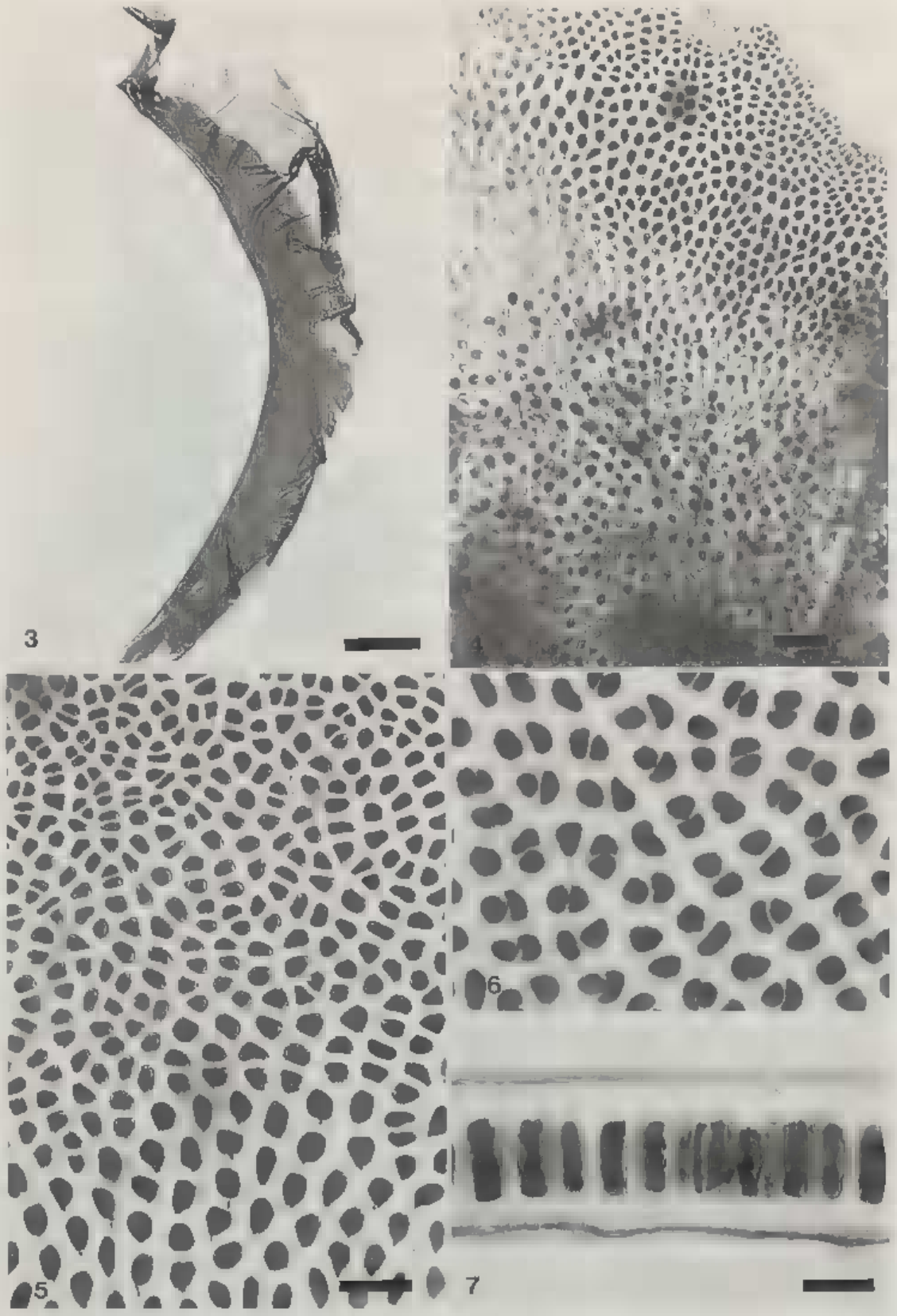
HOLOTYPE: Collected from the eulittoral zone, Sidmouth, Devon, Great Britain, by Juliet Brodie, 9.x.1996. Male plant (Fig. 1) dried on a single herbarium sheet with one other female specimen; deposited in the Natural History Museum, London (BM).
ISOTYPES: Laboratoire de Cryptogamie, Muséum National d'Histoire Naturelle, Paris (PC), Botanischer Garten und Botanischen Museum, Berlin-Dahlem (B), Atlantic Research Laboratory, Halifax, Nova Scotia (NRCC), Botany Department, University College, Galway, Ireland (GALW), The Botany Department, The Faculty of Science, Hokkaido University, Sapporo, Japan (SAP) and Biologische Anstalt Helgoland. Abbreviations follow Holmgren *et al.* (1990).
ETYMOLOGY: The name *dioica* refers to the dioecious nature of reproductive fronds of this species.

Description

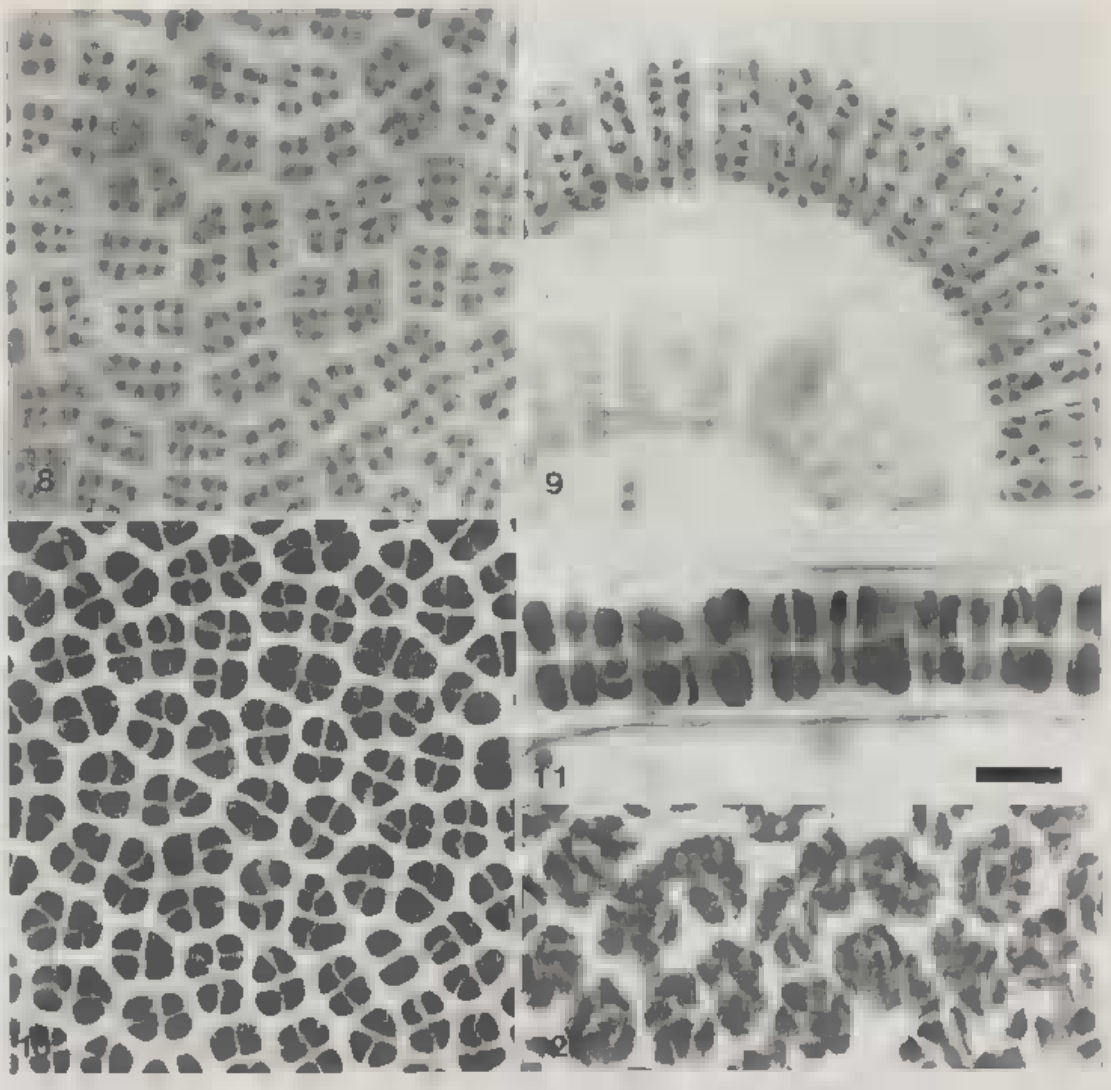
Thallus of blade phase with a minute discoid holdfast and stipe expanding into a thin, but not typically translucent blade which folds in half longitudinally when held

Figs 1-2. Fig. 1. Holotype of *Porphyra dioica*. Scale bar = 4 cm. Fig. 2. Neotype of *Porphyra purpurea*. Scale as in Fig. 1.

vertically (Fig. 3); blades glossy, sometimes laciniate, up to 270 mm tall, to 270 mm broad and to 48-80 µm thick, usually light to dark olive green in summer, purple-brown in winter; margin, sometimes ruffled. Usually one fully developed frond develops from each holdfast, although a tiny frond (4-6 mm long) to several well developed blades, up to approximately 116 mm tall to 40 mm broad, may also be present arising from the holdfast. Holdfast and stipe of narrow, elongate rhizoidal cells each terminating in a club hea (Figs 4, 5); blade one cell thick, parenchymatous in structure; above the rhizoidal base is a narrow region of single cells, 20-32 µm in diameter in surface view (Fig. 5), which grades into pairs of oval to rectangular or crescent-shaped cells which form the main body of the blade (Fig. 6). In the central part of the blade these vegetative cells are 10-16 µm in diameter in surface view, and 36-40 µm tall by 12-14 µm broad in TS (Fig. 7). Plants dioecious; male plants tend to be narrower and more laciniate than female plants. Spermatangia in yellowish-white sori along the margins of the male gametophyte. In surface view spermatangial packets are in groups of 8 (2 x 4) (Fig. 8); each of these cells divides to give 8 cells in TS (Fig. 9), making 64 spermatia in each spermatangial packet. Carpogonia continuous in reddish-brown marginal sori. Carposporangial packets 20-22 µm in diameter, appearing as groups of 4 in surface view (Fig. 10); each of these cells dividing in the plane of the blade to give 2 cells (Fig. 11), making 8 carpospores in each carposporangium (Fig. 12). Carpospores germinating into a filamentous "*Conchocelis*" (Fig. 13), consisting of narrow, long-celled filaments, 4-8 µm broad and broader, conchosporangial branches, 16-20 µm broad (Figs 14, 15).



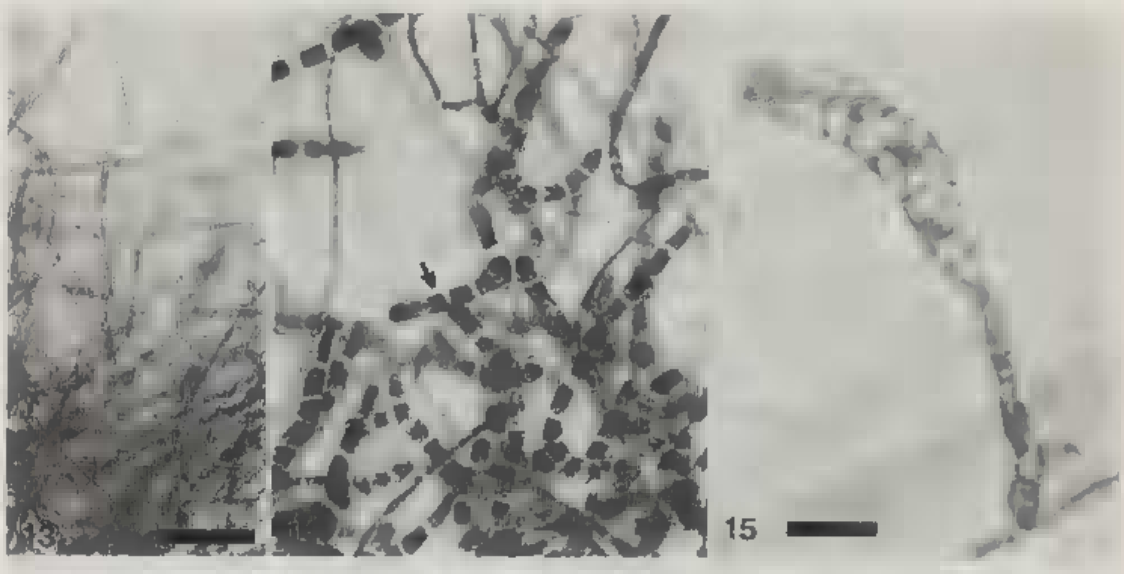
Figs 3-7. *Porphyra dioica* — vegetative morphology of blade phase. Fig. 3. Blade folded in half. Rhosneigr, Anglesey, Wales, 14.iv.1996. Scale bar = 2 cm. Fig. 4. Rhizoidal cells of holdfast grading into cells of blade in surface view. Scale bar = 100 µm. Fig. 5. Edge of rhizoidal region grading into area of single vegetative cells of blade in surface view. Scale bar = 50 µm. Fig. 6. Pairs of vegetative cells in surface view. Fig. 7.TS vegetative cells. Scale bar = 25 µm; also applies to Fig. 6.



Figs 8-12. *Porphyra dioica* - reproductive morphology of blade phase. Fig. 8. Spermatangial packets in surface view. Fig. 9. TS spermatangial packets. Fig. 10. Carpogonial packets in surface view. Fig. 11. TS carposporangial packets. Fig. 12. Carposporangial packets in oblique section, each containing 8 carpospores. Scale bar = 25 μm; applies to all figures.

Blade-phase epilithic on boulders and pebbles in sand on exposed shores or more exposed regions of sheltered shores; often dominating boulders, sometimes with tips of fronds trailing in water around boulders; appearing black and glossy *en-masse* when semi-dried; lower-midlittoral level; also occurring more sparsely amongst *Enteromorpha* spp. higher in the lower part of the upper littoral where it tends to be paler, smaller and often highly laciniate and may sometimes appear spiralled.

We have examined material from Britain (Sussex, Devon, Cornwall, Glamorgan, Pembrokeshire, Anglesey, Aberdeenshire, Norfolk) and Ireland (Co. Clare). We have also identified material from the Faroes, Helgoland and Portugal. The full range of this species in the northern Atlantic is currently unknown.



Figs 13-15. *Porphyra dioica*, "*Conchocelis*"-phase. Fig. 13.Narrow, vegetative filaments. Scale bar = 50 µm; also applies to Fig. 14. Fig. 14.Conchosporangial branches (arrow). Fig. 15. Conchosporangial branch. Scale bar = 25 µm.

Plants of the blade-phase are found throughout the year; blades, probably annual; reproductive structures can be found throughout the year, although they appear to be at the end of their viability by early autumn when many tattered fronds bearing epiphytes occur; young plants are present in the autumn and probably mature over winter. The "*Conchocelis*"-phase has not been recognised in the field.

Herbarium specimens become purple to dark purple on drying and can acquire a glossy sheen. They adhere well but do not become integrated with the paper as happens with some *Porphyra* spp.

***Porphyra purpurea* (Roth) C. Ag., sensu stricto**

Diagnosis

Blade translucent, usually entire, elliptical to obovate, up to 260 mm long and 117 mm broad, brown to reddish-brown; monostromatic, cells 10-16 µm in surface diameter, 28-30 µm long by 8-12 µm broad in TS. Thalli monoecious; much of the frond becoming fertile; spermatangial zone yellow-white, carpogonial zone reddish-brown; spermatangial packets 22-26 µm tall by 15-16 µm broad in surface view, containing 64 spermatia; carposporangial packets 20-23 µm tall by 18-23 µm broad in surface view containing 16 carpospores. "*Conchocelis*" filamentous, filaments 4-8 µm in diameter.

NEOTYPE: (Fig. 2) Collected from the upper eulittoral zone, NE-intertidal (Nord-Ost Watt), Helgoland, by Andreas Wagner, 17.x.1996. Fertile plant (Fig. 2), dried on a single herbarium sheet with two other fertile specimens (one lacking holdfast); deposited in the Natural History Museum, London (BM).
ISONEOTYPES: PC, B, NRCC, GALW, SAP and Biologische Anstalt Helgoland.

Porphyra purpurea was first described by Roth (1788, p. 524, as *Ulva purpureo-violacea*) and his original specimens came from Ritzebüttel near Cuxhaven, north Germany. His description concerns only external features and it is insufficient to define a species within the genus *Porphyra*. Unfortunately his herbarium was destroyed in Berlin in 1943 (Hiepko, 1987). We therefore decided to select a neotype and it seemed appropriate to follow Kornmann & Sahling's (1991) interpretation of Roth's species. We have chosen specimens from Helgoland, their working area, which is reasonably close to the original type locality.

Description

Thallus with a minute holdfast and stipe extending rapidly into a thin, slightly glossy, translucent blade; blade narrow to broad and almost ovate, up to 260 mm long, 17 mm broad and to 40-72 μm thick, reddish-brown to brown; margins occasionally ruffled; not usually laciniate; may have more than one blade from holdfast. Holdfast and stipe of narrow, elongate rhizoidal cells, each terminating in a club head (Fig. 16); blade one cell thick, parenchymatous in structure; above the rhizoidal base is a narrow region of single cells, 18-32 μm in diameter in surface view (Fig. 16), which grade into pairs of oval to crescent-shaped cells which form the main body of the blade (Fig. 17). In the central part of the blade these vegetative cells are 10-16 μm in diameter in surface view, and 28-30 μm long by 8-12 μm wide in TS (Fig. 18). Monoecious; spermatangial and carposporangial region often of unequal size (Fig. 2); spermatangial region pale yellow, carposporangial region dark red. In surface view spermatangial packets are in groups of 16 (Fig. 19); each of these cells divides to give 4 or 8 cells (Fig. 20), making 64-128 spermatia in each spermatangial packet. Carposporangial sori patchy; carposporangial packets appearing as groups of 4 in surface view (Fig. 21), 16-22 μm in diameter, each of these cells divides to give 4 cells (Fig. 22), making 16 carpospores in each packet (Fig. 23). Carpospores germinating into a filamentous "*Conchocelis*" (Fig. 23), consisting of narrow filaments, 4-8 μm broad and broader conchosporangial branches 16-24 μm broad (Figs 24, 25).

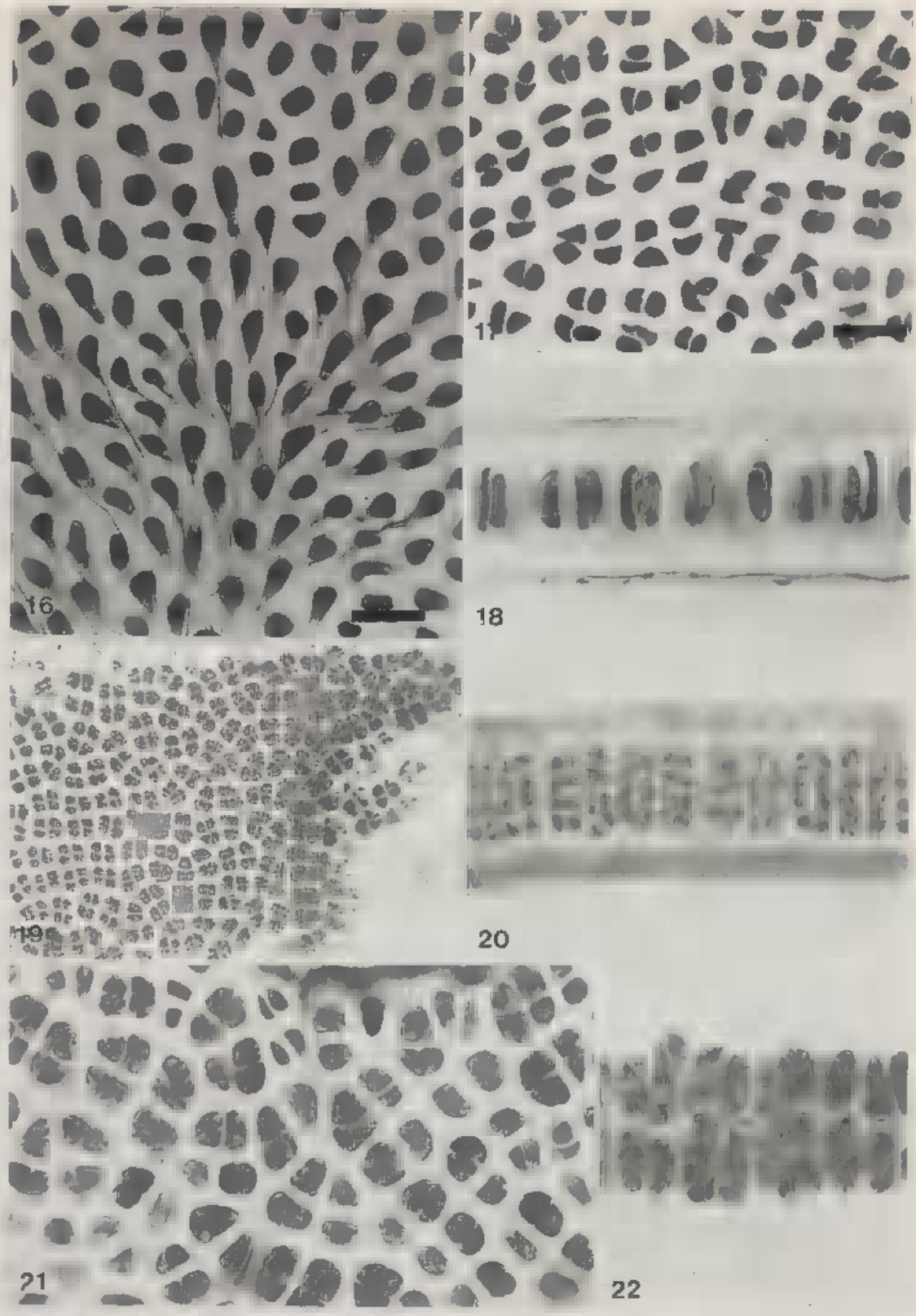
Blade phase epilithic on bedrock, boulders and pebbles often buried in sand; epizoic on barnacles; principally midlittoral; common on sheltered shores and extending up estuaries.

We have examined material from Britain (Sussex, Hampshire, Devon, Cornwall, Glamorgan, Pembrokeshire, Anglesey, Aberdeenshire, Kincardineshire, Norfolk) and Ireland (Co. Clare). We have also identified material from the Faroes and Helgoland. The full range of this species in the northern Atlantic is currently unknown.

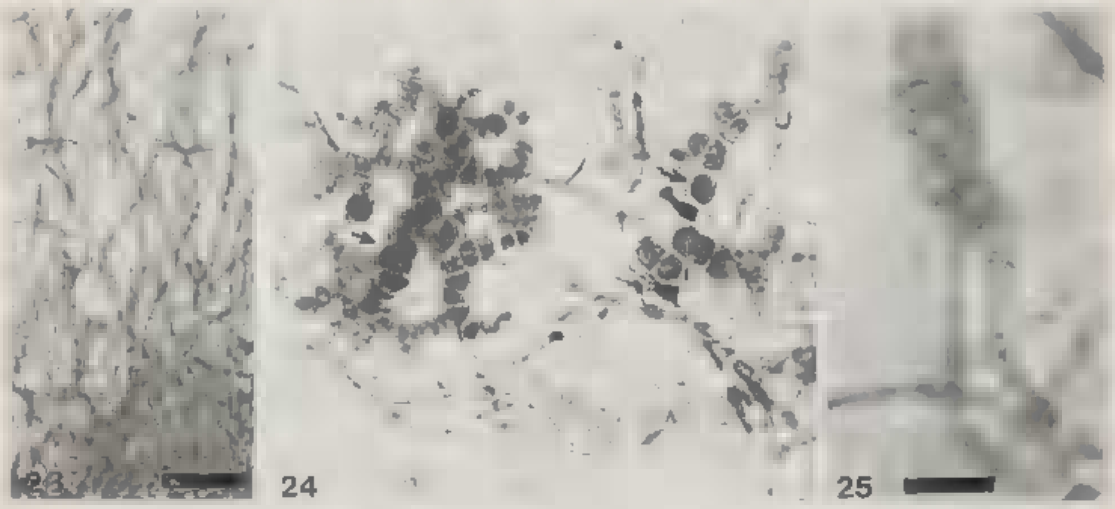
The blade phase occurs throughout the year and blades are probably annual; reproductive structures are found throughout the year with a peak in summer. The "*Conchocelis*"-phase has not been recognised in the field.

This species is morphologically highly variable. It is possible to find very narrow plants growing alongside much broader specimens; some individuals may have ruffled margins.

Herbarium specimens become brown to purple-brown on drying and may be matt to slightly glossy. They adhere well, but do not become integrated with the paper.



Figs 16-22. *Porphyra purpurea* - vegetative and reproductive morphology of blade phase. Fig. 16. Rhizoidal cells of holdfast grading into cells of blade. Scale bar = 50 mm; also applies to Fig. 19. Fig. 17. Pairs of vegetative cells. Scale bar = 25 mm; also applies to Figs 18, 20-22. Fig. 18. TS vegetative cells. Fig. 19. Spermatangial packets in surface view. Fig. 20. TS spermatangial packets. Fig. 21. Carpogonial packets in surface view, 16 carpospores per packet. Fig. 22. TS carposporangial packets.



Figs 23-25. *Porphyra purpurea*, "*Conchocelis*"-phase. Fig. 23.Narrow filaments of "*Conchocelis*". Scale bar = 50 μm; also applies to Fig. 24. Fig. 24. Conchosporangial branches (arrow). Fig. 25. Conchosporangial branch. Scale bar = 25 μm.

DISCUSSION

A comparison of the two species (Table 1), shows that, although superficially similar, they are separable with practice on the basis of colour and morphology. The olive-green to purple-brown plants of *P. dioica* tend to be slightly larger with frequently laciniate and thicker fronds than the brown to reddish-brown blades of *P. purpurea*. The two species differ reproductively: *P. dioica* is dioecious, whereas *P. purpurea* is monoecious. The derivation of spermatangial packets is different in the two species: in *P. dioica* they are in groups of 8 (2 x 4) in surface view each with 8 in TS, whereas in *P. purpurea* they are in 2 groups of 16 in surface view each with 4 or 8 in TS. *Porphyra dioica* has 8 carpospores in each carposporangial packet, whereas *P. purpurea* has 16. Carpospores in both species develop into a filamentous "*Conchocelis*"-phase with narrow vegetative and broad conchosporangial branches occurring in both species.

Although they can sometimes be found intermixed, the differences in shore level and exposure tolerance of the two species suggest ecological/physiological differences which require further study. The geographical distribution of both species also requires further investigation. It seems reasonable to assume that they both occur throughout Britain and Ireland in suitable habitats and we know they also extend to the Faroes and Helgoland. *Porphyra dioica* also occurs in Portugal. Reports of *P. purpurea* from elsewhere require confirmation. For example this species is reported to occur in the western North Atlantic from Arctic Canada and the Maritime provinces of Canada (Bird & McLachlan, 1992) but this report requires reinvestigation in the light of our data. The presence of *P. dioica* in the western Atlantic has not been ascertained.

A comparison of our material of both species with the descriptions given by Kornmann & Sahling (1991) show few differences. In *P. dioica* they reported the presence not only of carpospores but also of asexual spores, both of which gave rise to "*Concho-*

Characters	*Porphyra dioica*	*Porphyra purpurea*
Gross morphology	narrow-lanceolate to broadly ovate sometimes laciniate, folding in half	usually entire, elliptical to obovate
Colour (fresh)	olive-green/purple brown	reddish-brown/brown
Colour (dry)	purple-dark purple	brown/red-brown/purple-mauve
Cell layers	1	1
Frond thickness (μm)	40-80	48-72
Cell diameter (μm)	10-16	10-16
Cell dimensions in TS (μm)	36-40 x 12-14	28-30 x 8-12
Reproduction	dioecious	monoecious and autoecious[1]
Reproductive bodies	peripheral zone, upper part of frond	scattered
Spermatangial sori	packets of 64	packets of 64 or 12
Carposporangial sori	packets of ▮	packets of 16
Main littoral region	lower-middle	middle
Substrata	boulders/pebbles in sand	various: bedrock, boulders, shells e.g.limpets, barnacles
Exposure	more exposed	more sheltered
Plants present	all year	all year

Table 1. Table of characters for *Porphyra dioica* and *P. purpurea*. [1] Autoecious: reproductive bodies in separate male and female regions of a plant as opposed to synoecious, where they are intermingled.

celis" phases. Asexual spores were not observed in our plants of *P. dioica* from Britain. In *P. purpurea* there are differences in female reproduction between their material and ours. In the former, carposporangial packets contain 4 spores in surface view and are arranged in two layers, making 8 carpospores, whereas in our material, 16 carpospores develop per packet. Without following individual packets, it is impossible to tell whether or not those with 8 are fully mature. The observations suggest that there is some variation within these species, but it is premature to draw conclusions until further material has been examined. It should be noted that the RUBISCO spacer sequence for *P. dioica* from Helgoland is identical with specimens of this species we have collected elsewhere and that the sequence for *P. purpurea* is the same as material from other localities (Brodie *et al.*, 1996).

In view of the distinct ontogeny of carposporangia in *Porphyra* and other related genera, Guiry (1990) proposed the introduction of the term zygotosporangia for such sporangia i.e. those formed within a fertilized carpogonium from the zygote or by direct division of the zygote. However, we have decided to use the term carposporangia in this paper in view of the current lack of equivalent terminology in describing spermatangia and carpogonia.

Distinguishing *P. dioica* and *P. purpurea* is not easy, particularly for single, sterile specimens. Further studies that will provide valuable data in this regard include chromosome numbers, and consideration of ecology and physiology. A detailed comparison of *P. dioica* and *P. purpurea* with other species of *Porphyra* occurring in European waters and elsewhere awaits similar studies.

Analysis of sequence data for the chloroplast-borne RUBISCO spacer revealed previously that a single transition separates *P. dioica* from *P. purpurea* (Brodie *et al.*, 1996). The RUBISCO spacer sequence data provided evidence to support our search for morphological characters to distinguish between species within this genus. The combined data presented here confirm the conclusion of Kornmann & Sahling (1991) that "*P. laciniata* [now *P. dioica*] — formerly considered synonymous with *P. purpurea* — is an independent species."

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